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A STUDY OF THE BIOLOGY OF SPECIES OF THE GENUS *MESOPOLOBUS* WESTWOOD (HYMENOPTERA: PTEROMALIDAE) ASSOCIATED WITH CYNIPID GALLS ON OAK

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With 11 Text-figures

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I. Introduction

Gall wasps (Hymenoptera, Cynipidae) induce the growth of galls on a variety of plants and their immature stages are passed inside these galls. Many other species of Hymenoptera feed either on the vegetable tissue of the gall, or on the other inhabitants, or on both. These species belong almost entirely to the Chalcidoidea or to the tribe Synergini of the Cynipidae.

Species of the genus *Mesopolobus* make up a large fraction of the Chalcidoid species inhabiting Cynipid oak galls. Their larvae are ectophagous, feeding on larvae, pupae or sometimes even adults of other gall inhabitants. Only one adult *Mesopolobus* emerges from a gall cell, therefore only one emerges from a gall, unless the gall is plurilocular or has been attacked by a species of *Synergus* which makes subsidiary cells.

Each *Mesopolobus* species attacks a range of galls, and is polyphagous in galls within this range, apparently feeding on any other species, parasites or gall makers, which are available. Frequently first instar *Mesopolobus* larvae were found feeding

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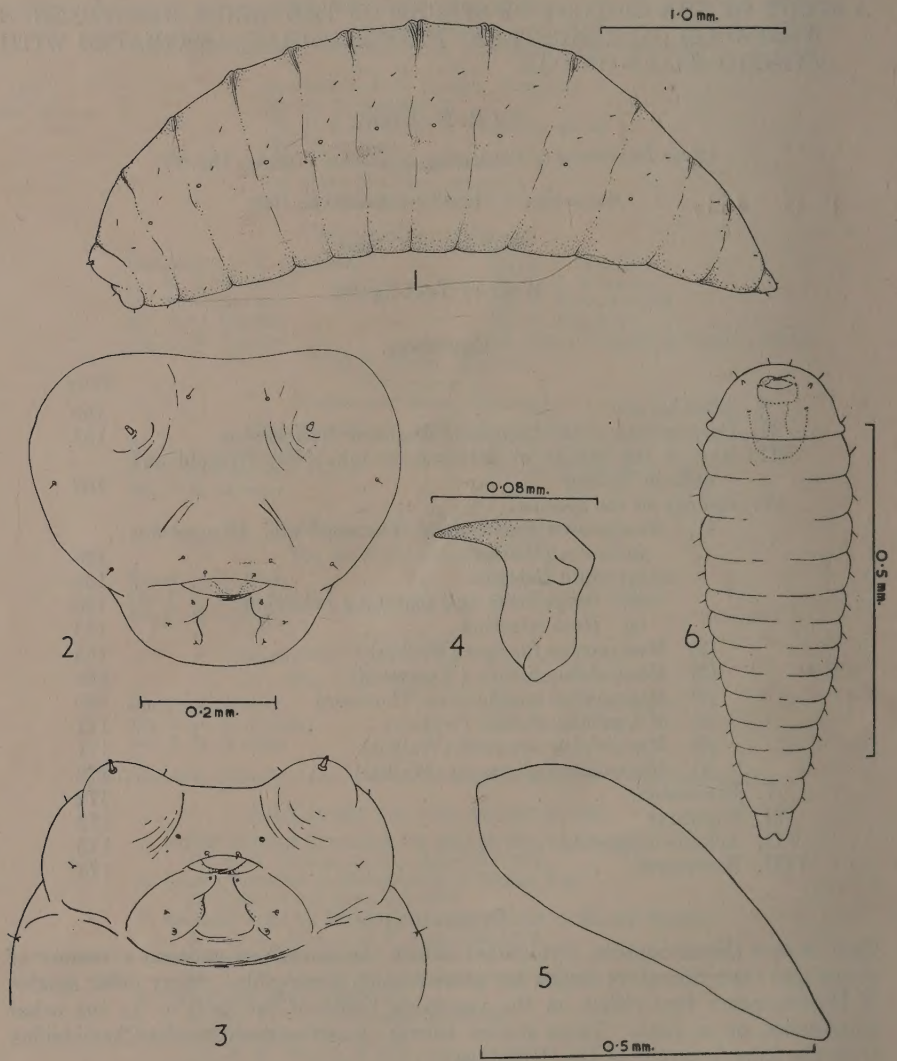
on older *Mesopolobus* larvae. However, interspecific destruction is minimised by the adoption of a different host–gall range by each species. The factors which determine the extent of these host–gall ranges are considered in this paper.



Figs. 1–6.—*Mesopolobus jucundus* (Walk.): (1) Fully grown larva. (2–3) Head of fully grown larva: (2) frontal view; (3) ventral view. (4) Larval mandible. (5) Egg. (6) First instar larva, dorsal view.

At least eight *Mesopolobus* species inhabit Cynipid galls on oak in Britain. These are *M. fasciiventris* Westwood, *M. jucundus* (Walker), *M. tibialis* (Westwood), *M. dubius* (Walker), *M. xanthocerus* (Thomson), *M. fuscipes* (Walker), *M. amaenus* (Walker) and *M. albitarsus* (Walker). Only one of these species, *M. jucundus*, has been recorded (Askew, 1960) from Cynipid galls on plants other than oak. In these latter galls their place would appear to be taken by species of the genus *Habrocytus* Thomson, this genus also being placed in the family Pteromalidae.

The taxonomy of *Mesopolobus* has been dealt with in a series of papers by von Rosen (1958, 1959, 1960*a* and *b*). The genus was erected by Westwood in 1833 for a single species, *M. fasciiventris*, but von Rosen has greatly increased its size by describing new species and by including in *Mesopolobus* several genera kept separate by other authors (*e.g.* Graham, 1957). In the present work von Rosen's concept of the genus is followed.

Most of the collections of galls, and all the field observations, were made in Wytham Wood, Berkshire, and unless stated otherwise all the records pertain to this locality. Use was also made of information on the labels of specimens in the following collections : British Museum (Nat. Hist.) ; Hope Department, Oxford ; Oak Survey collection, compiled by Professor G. C. Varley from specimens collected in Wytham Wood ; personal collection of Mr. G. R. Gradwell ; and the personal collection of Dr. M. F. Claridge.

The flight periods of the species are shown by histograms, the months on the horizontal axis being each divided into four periods, and the number of specimens taken in these periods is indicated on the vertical axis. Only insects taken on oak in Wytham Wood between August 17th, 1957 and February 1st, 1960 are included, unless stated otherwise in the text. Visits to Wytham Wood were made as regularly as possible ; fluctuations in numbers of *Mesopolobus* taken due to variation in the number of collecting trips per period do not obscure the actual flight periods of the species. A sweep net and beating tray were primarily used in making the collections. The oak referred to is *Quercus robur* L., unless *Q. cerris* L. is specifically mentioned.

II. Descriptions of the Immature Stages of *Mesopolobus*

The immature stages are known for only four of the species, *M. jucundus*, *M. fasciiventris*, *M. tibialis* and *M. fuscipes*. Their eggs were found to be similar. They appear white with unsculptured and unpigmented chorions, and they are elliptical, tapering more towards the posterior end, and devoid of filamentous projections. The anterior end is bluntly rounded with only a very slight protuberance. The egg of *M. jucundus* (fig. 5) is 0·65 mm. long with a maximum breadth of 0·28 mm.

The first instar larvae of the four species are also very much alike and typical of the ectophagous Pteromalidae. The first instar larva of *M. jucundus* (fig. 6), which has been examined in most detail, has 13 segments after the head, each of which (except the last) bears a pair of short hairs. The hairs on the first body segment are directed forwards, those on the other segments are directed backwards. The last segment is bilobed. The head bears a pair of rudimentary antennae and three pairs of hairs. The mandibles are small and pointed. In life, the tentorium can sometimes be seen extending backwards in a U-shaped arc. The first instar larva of *M. jucundus* is similar to that of *Habrocytus trypetae* Thomson (Pteromalidae) described by Varley (1937), differing most obviously in having hairs on body segments 1–12 instead of only 1–6.

The last stage larvae of *M. jucundus* (fig. 1), *M. fasciiventris*, *M. tibialis* and *M. fuscipes* are also very much alike, as in fact are most ectophagous Pteromalid larvae. They are characterised by their sparse clothing of short hairs and by the prominence of their antennae. The fully grown larva of *M. jucundus* measures about 4 mm. in length. It is white in colour and there are 13 body segments of which the first bears four pairs of short hairs, the second and the last bear three pairs and the remainder two pairs. Spiracles are situated towards the anterior borders of body segments 2–10. The head (figs. 2 and 3) bears a pair of antennae at the apex of two large, rounded prominences on the dorsal half of the frons. The mandibles (fig. 4) are simple and acute. There are three pairs of short setae on the frons and two more pairs on the labrum.

III. Key to the Species of *Mesopolobus* Inhabiting Cynipid Oak Galls in Britain

Females

1 Body elongate, gaster longer than head, thorax and propodeum together; head in dorsal view with width of postorbital region rather more than half transverse diameter of eye; body colour green. (Antennae with 2 annelli) 7
– Body less elongate, gaster shorter than head, thorax and propodeum together; head in dorsal view with width of postorbital region usually much less than half transverse diameter of eye (if about equal to half transverse diameter of eye (*amaenus*), then antennae have 3 annelli); body colour usually more or less bronze or (*albitarsus*) blueish 2
2 Antennae with 2 annelli . . . . . **tibialis** (Westwood)
– Antennae with 3 annelli 3
3 Pronotal collar broad, about equal in width medially to distance between lateral ocelli and orbit . . . . . **amaenus** (Walker)
– Pronotal collar narrow, median width much less than distance between lateral ocelli and orbit 4
4 Tibiae uniformly infuscate; stigmal vein rather strongly curved **fuscipes** (Walker)
– Tibiae testaceous or yellow; stigmal vein only slightly curved 5
5 Valvulae ventrales long, about two-thirds length of gaster **xanthocerus** (Thomson)
– Valvulae ventrales shorter, at most only slightly over half length of gaster . 6
6 Body colour blueish; all funicle segments longer than broad . **albitarsus** (Walker)
– Body colour bronze-green; distal funicle segments broader than long **dubius** (Walker)
7 Clypeus with strong median incision . . . . . **jucundus** (Walker)
– Clypeus with slight median incision . . . . . **fasciiventris** Westwood

Males

1 Middle tibiae each with dark spot distally 2
– Middle tibiae without dark spot distally 4
2 Middle tibiae with dark spot borne on prominent tongue-like projection . 3
– Middle tibiae with dark spot not borne on tongue-like projection and with orange and brown stripes . . . . . **tibialis** (Westwood)
3 Middle tibiae each with an orange stripe . . . . . **xanthocerus** (Thomson)
– Middle tibiae uniformly yellow . . . . . **fasciiventris** Westwood
4 Middle tibiae with orange and brown stripes . . . . . **fuscipes** (Walker)
– Middle tibiae without coloured stripes 5
5 Pronotal collar broad, about equal in width medially to distance between lateral ocelli and orbit . . . . . **amaenus** (Walker)
– Pronotal collar narrow, median width much less than distance between lateral ocelli and orbit 6
6 Antennae with 2 annelli and uniformly yellow . . . . . **jucundus** (Walker)
– Antennae with 3 annelli 7
7 Antennae with last 2 funicle segments broader than long; third funicle segment and first two claval segments fuscous . . . . . **dubius** (Walker)
– Antennae with all funicle segments longer than broad . . **albitarsus** (Walker)

I have not seen a male of *M. albitarsus*. The characters used in the key to distinguish it are taken from the work of von Rosen (1958).

IV. Biology of the Species

(1) Mesopolobus fasciiventris *Westwood and* Mesopolobus jucundus (*Walker*)

(a) *Life Histories*

M. fasciiventris and *M. jucundus* are included in Graham's definition of the genus *Mesopolobus* and biologically, as well as morphologically, they are similar.

Field captures of *M. fasciiventris* and *M. jucundus* are shown in figure 7 and the life-cycle of *M. fasciiventris* in figure 8. The generations of the two species are almost synchronous. Each has a spring generation, containing a large percentage of males, which in *M. jucundus* was found in the field from the third week in April to the last week in June (although the single male taken in the first week of July may belong to this generation), and in *M. fasciiventris* from the second week in May to the last week in June. This is followed by a second generation in flight in the latter half of July, and by a third generation, containing only a few males, which was found from September to November in the case of *M. fasciiventris* and from August to November in the case of *M. jucundus* ; however, it is possible that insects caught in late October and in November represent a partial fourth generation.

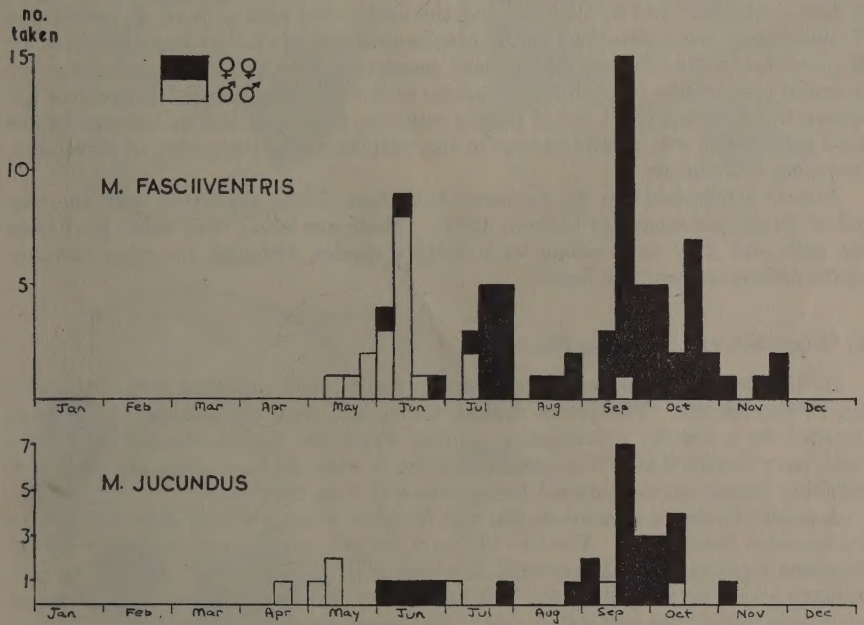


FIG. 7.—Field captures of *Mesopolobus fasciiventris* Westw. and *M. jucundus* (Walk.).

Both species attack the inhabitants of a wide range of galls. The actual numbers of each species found associated with the different galls are given in Table III.

The spring (first) generations of both species were reared from galls of *Cynips divisa* Htg., *C. longiventris* Htg., *C. quercus-folii* L. and *Andricus ostreus* (Htg.), gathered in the autumn and winter. In addition, many overwintering *M. jucundus* were bred from galls of *A. kollari* Htg., and a single specimen from an oak-apple gall of *Biorhiza pallida* (Oliv.) which was still attached to the tree in December. One female specimen of *M. jucundus* was also bred from a gall of *A. callidoma* (Htg.) gathered in October, and another was found dead in a gall of *A. solitarius* (Fonsc.) collected at Hell Coppice, Buckinghamshire, in May. A female *M. jucundus* in the British Museum (Nat. Hist.) is labelled as emerging from a gall of *A. inflator* f. *globuli* (Htg.) from Burnham Beeches, Buckinghamshire. A single specimen of *M. fasciiventris* in the Oak Survey collection is labelled as being bred from a gall of *Neuroterus quercus-baccarum* f. *lenticularis* (Oliv.). No date is given, but certainly it must have overwintered in this gall, which is only available to third generation *M. fasciiventris* in autumn. Galls of *N. numismalis* (Geoff.) and *N. albipes* f. *laeviusculus* Schenck also yielded *M. fasciiventris* in spring.

Adults of the first generation of the year attack the contents of new galls of the summer generations of various oak Cynipidae. Both species were bred from galls of *A. curvator* Htg., and a female *M. jucundus* was observed drilling into a gall of this species. *M. jucundus* also emerged from leaf galls of *N. quercus-baccarum* (L.) and from *B. pallida* galls in July, and *M. fasciiventris* emerged from galls of *N. numismalis* f. *vesicator* (Schl.) and *N. albipes* (Schenck) at this time. *M. fasciiventris* were found drilling into galls of *N. numismalis* f. *vesicator* in early June.

Insects of the second generations of both species were observed drilling galls of *C. divisa*. In autumn *M. jucundus* was bred from *A. kollari* galls, *M. fasciiventris* from *C. longiventris* galls, and both species from *C. divisa* galls.

The third generations attack the same types of galls from which they have emerged. Many specimens of both species were found drilling into *C. divisa* galls in late September and in October, and the author has seen galls of *A. ostreus* and *N. numismalis* being attacked by *M. fasciiventris*, and *A. kollari* being attacked by *M. jucundus*. The offspring of the third generations pass the winter as fully-grown larvae to produce the first adult generations in the following spring. There does not appear to be a diapause. Adult insects resulting from eggs laid in autumn by the third generations will usually emerge in the warmth of the laboratory in November, December or January.

Insects attributable to *M. jucundus* have been found associated with the rose gall of *Diplolepis rosae* (L.) (Askew, 1960). These are larger than those bred from oak galls and they may belong to a distinct species, although no other morphological differences could be found.

(b) *Oviposition and Searching Behaviour*

In the laboratory, females of both species readily attack detached galls of *C. divisa* and *C. longiventris*. The act of drilling into a gall with the ovipositor is always preceded by a lengthy investigation, during which the female *Mesopolobus* slowly walks over the surface of the gall, drumming it with the tips of its antennae. A searching female ignores exposed larvae removed from their galls.

A gall of *C. divisa* was cut in two and found to contain a fully-grown *Eurytoma brunniventris* Ratz. larva. The two halves of the gall were pinned together with the *Eurytoma* larva inside and presented to a female *M. fasciiventris*. After some preliminary attempts at drilling the gall at different points on its surface the insect eventually pierced the gall wall in one of the halves not far from the line of division. The other half of the gall was then removed and the ovipositor of the *Mesopolobus* could be seen penetrating the *Eurytoma* larva, which was wriggling. After eight minutes the ovipositor was withdrawn from the larva and from the gall. No eggs were deposited. The *Eurytoma* larva was examined and found to be paralysed. Healthy larvae twist and bend their bodies quite vigorously when touched, but the only movement made by the stung larva was a spasmodic working of the mandibles.

The eggs are laid, usually singly, on the paralysed body of the host.

In the field, females of *M. fasciiventris* and *M. jucundus* were observed flying up and down and round oak trees, keeping within a few centimetres of the peripheral foliage. They were orientated so as to face this foliage, and often they alighted on leaves or twigs, which were examined with their antennae. Females were occasionally seen to make runs at other searching Chalcids, causing them to jump away. Both species have been seen searching trees on which no galls could be found. A small branch, bearing galls of *Cynips divisa*, which had been seen to be attacked by *Mesopolobus*, was sleeved in muslin. Occasionally both species of *Mesopolobus* flew near to it, but they did not check their flight or show any interest in the sleeve. Further, small muslin bags containing large numbers of galls of a variety of Cynipids, suspended by thread amongst the foliage of an oak tree, were completely ignored by searching

Mesopolobus, and fresh galls in olfactometers, both of the Y-tube type and the type used by Varley and Edwards (1953), were ignored by *Mesopolobus* of both species, which are therefore not guided in their search for host galls by an olfactory sense. When female *Mesopolobus* walk over leaves bearing galls they seem to be unaware of the

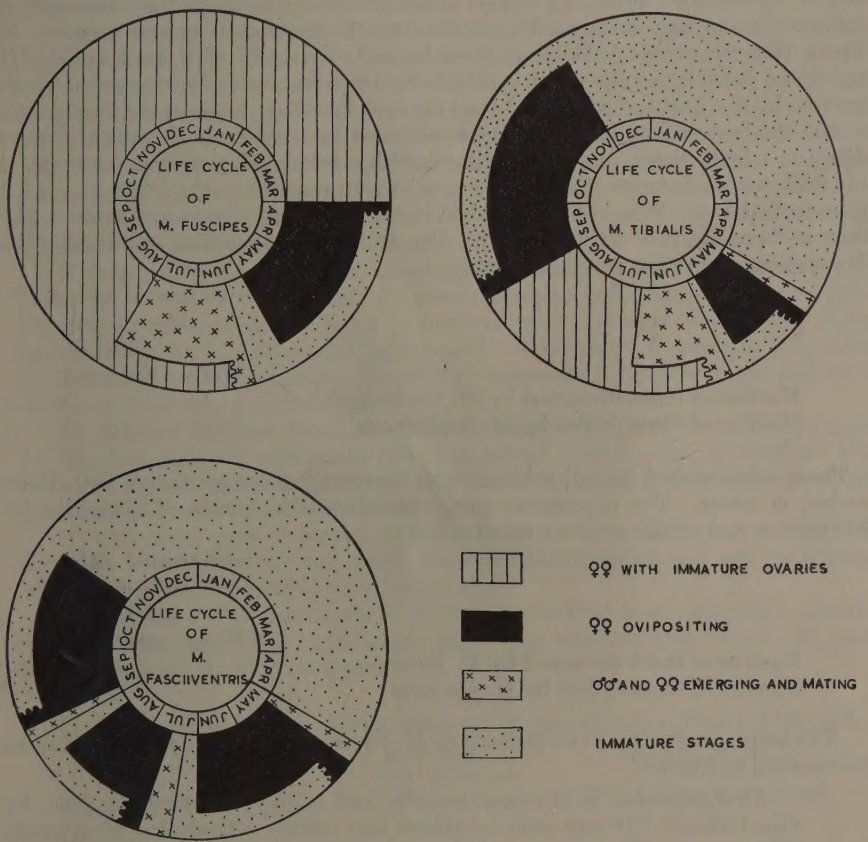

LIFE CYCLE OF M. FUSCIPES
LIFE CYCLE OF M. TIBIALIS
LIFE CYCLE OF M. FASCIIVENTRIS
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
♀♀ WITH IMMATURE OVARIES
♀♀ OVIPOSITING
♂♂ AND ♀♀ EMERGING AND MATING
IMMATURE STAGES

FIG. 8.—Diagrams showing the life-cycles of *Mesopolobus fuscipes* (Walk.), *M. tibialis* (Westw.) and *M. fasciiventris* Westw.

presence of the galls until they pass within about 4 mm. of one, when they suddenly deviate from their original course and walk directly up to the gall. The sense of sight attracts the parasite to the gall from a short range only and releases the drumming response. Galls which are indistinctly separated from the normal plant tissue, for example those of *N. numismalis* f. *vesicator*, are not perceived until the parasites are actually walking on them, when the shape, odour or texture of the gall surface apparently elicits the drumming reaction.

Varley (1941) has shown that *Eurytoma curta* Walker, which attacks the Trypetid fly *Urophora jaceana* Hering living in flower heads of black knapweed (*Centaurea nigra* L.), recognises the flower heads as objects of special significance, " probably . . . by sight, though it is quite possible that smell plays some part also ". Searching females of *Habrocytus albipennis* (Walker), which attack the Trypetid *Trypeta tussilaginis* (F.) in flower heads of burdock (*Arctium* sp.), were observed by the author flying from flower head to flower head. Plantain (*Plantago* sp.) was growing beside

the burdock and occasionally a female would fly towards this instead of the burdock, only turning away and back to the burdock when within about half a centimetre of the plantain head. These instances stress the importance of vision in the search for hosts by some Chalcidoidea.

Small balls of plasticine were frequently drummed by female *M. fasciiventris* and *M. jucundus* for quite long periods in the laboratory, although they were seldom drilled. In the field a female *M. jucundus* was observed drilling into a cocoon of *Praon* (Hymenoptera : Aphidiidae) spun beneath the body of a dead aphid. It was found possible to induce both species to drill into the seeds of goose grass (*Galium aparine* L.) the hooks of which had been crushed by rolling between the fingers, and which had been soaked in a gall extract obtained by crushing fresh galls of *Cynips divisa* in a little water. In an experiment with a female *M. fasciiventris* caught in the field, ten seeds (mean diameter 3·6 mm.) were presented to the insect in a small glass-topped box. Five had been soaked in tap water and five in gall extract, and their surfaces had been allowed to dry. The drumming and drilling responses of the *Mesopolobus* in an hour are shown below :

	Seeds treated with	
	Water	Gall Extract
Number of times drummed by *M. fasciiventris* .	4	16
Number of times drilled by *M. fasciiventris* .	2	13

Those seeds soaked in gall extract were apparently more attractive than those soaked in water. The experiment was repeated with a female *M. jucundus* for 90 minutes, and similar results were obtained :

	Seeds treated with	
	Water	Gall extract
Number of times drummed by *M. jucundus* .	1	6
Number of times drilled by *M. jucundus* . .	.	4

The stages leading up to oviposition in *M. fasciiventris* and *M. jucundus* may be summarised as follows :

(i) *Mesopolobus* is attracted to galls, and to objects resembling galls, by visual stimuli. It may come by chance into contact with the less conspicuous galls.

(ii) It walks on to the gall, or gall-like object, and rapidly taps the surface (drums) all over with its antennae. The experiments with goose grass seeds show that galls may be distinguished from other objects by antennal chemoreceptors. Galls a year or more old are rejected, probably because they have lost their odour. Further, galls with pieces missing from their walls (*e.g.* those with emergence holes) are usually, but not invariably, rejected during this investigation ; on one occasion a female *M. fasciiventris* was observed in the field drilling into a gall of *C. divisa* from which the occupant had emerged.

(iii) The insect drills into the wall of the gall with its ovipositor. In the case of hard, mature galls of *Cynips divisa*, *Andricus kollari* etc., several attempts are usually made at different points on the surface before the gall wall is finally penetrated, and some galls are rejected, presumably because of their excessive hardness. *Mesopolobus* sometimes drills into empty galls.

(iv) The ovipositor feels inside the gall, and if a larva is present it is stung, and oviposition usually follows on the surface of the host. Sense organs on the ovipositor tip must detect the present of host larvae.

(c) *Host Selection*

The numbers of specimens of *M. fasciiventris* and *M. jucundus* bred from various galls are given in Table III. The host–gall ranges of the two species are similar but not identical. In most types of gall one species predominates, and this minimises interspecific destruction. What factors bring about this partial separation of the immature populations of the two species?

(i) *Gall contents.*—Although the galls of many Cynipid species are host to one of these species of *Mesopolobus* more frequently than the other, of those galls from which large numbers of these species have been bred, only the galls of *A. kollari* and *B. pallida* have produced one species (*M. jucundus*) to the complete exclusion of the other. This suggests that either species is capable of development in most if not all galls. A single female *M. fasciiventris* in the laboratory laid eggs on larvae of *Synergus pallicornis* Htg., *Torymus* sp. and *Eurytoma brunniventris* on three consecutive days. Both *M. fasciiventris* and *M. jucundus* have been found to be polyphagous in galls, seemingly attacking any species that may be present.

M. fasciiventris has been found attacking *Eurytoma brunniventris* Ratz. larvae and pupae (*A. ostreus*, *C. divisa* galls), *Torymus cingulatus* Boh. larvae (*A. ostreus* galls), *Tetrastichus aethiops* (Zett.) larva (*A. ostreus* gall), *Synergus albipes* Htg. larvae (*A. ostreus* galls), *S. pallicornis* Htg. larvae (*C. divisa* galls), *S. nervosus* Htg. larvae (*C. divisa*, *C. longiventris* galls), *Neuroterus numismalis* f. *vesicator* pupae and larvae of *Mesopolobus* sp. (*A. ostreus* galls).

M. jucundus has been found attacking *Synergus gallae-pomiformis* (Fonsc.) larvae (*A. callidoma* gall), *S. umbraculus* (Oliv.) larvae (*A. kollari* galls), *S. reinhardi* Mayr larvae (*A. kollari* galls), *S. pallicornis* Htg. larvae (*C. divisa* galls), *Andricus curvator* pupa and *Neuroterus quercus-baccarum* pupae.

No gall would seem to escape attack because the larva inside it is unsuitable as food. It is evidently the gall itself, the vegetable structure and not its contents, which determines its liability to be attacked.

(ii) *Gall size.*—The proportions of the two species bred from oak galls is related to the sizes of the galls (Table I), the larger galls being attacked more often by *M. jucundus*, the smaller by *M. fasciiventris*.

TABLE I.—*Numbers of* M. fasciiventris *and* M. jucundus *bred from oak leaf galls*

Host galls	Mean length of fully grown gall (mm.)	Number of bred	
		M. fasciiventris	*M. jucundus*
N. albipes	1·8	5	.
A. ostreus	2·0	60	4
N. a. f. *laeviusculus*	2·2	1	.
N. numismalis	2·2	3	.
N. q-b. f. *lenticularis*	3·0	1	.
N. n. f. *vesicator*	3·1	19	.
C. divisa	3·2	153	54
C. longiventris	3·7	21	7
A. curvator	6·0	9	18
N. quercus-baccarum	6·7	.	2
C. quercus-folii	10·4	7*	5

* The high proportion of *M. fasciiventris* in *C. quercus-folii* galls is due to the flight period of the second generation of the *Mesopolobus* coinciding with an early stage of growth of the galls.

Considering a gall size of 5·0 mm. as the division between large and small galls, *M. fasciiventris* was bred in a greater proportion from small galls and *M. jucundus* in greater proportion from large galls ($P < 0{\cdot}001$).

Both *M. fasciiventris* and *M. jucundus*, enclosed in a small, glass-topped box, run towards spherical objects stuck to the glass lid of the box. Occasionally these would be drummed and mounted. A series of ten red plasticine balls were made with

diameters of 1 mm., 2 mm., 3 mm., 4 mm. ... 10 mm. These were stuck to the glass lid of the box with a small spot of seccotine. The box was illuminated directly from above and surrounded by sheets of white paper to minimise any reflection of the balls in the glass. A single female *Mesopolobus* was introduced at a time, and note was made of the balls which it approached after deviating from its original course. The experiment was conducted four times, each time with a different insect, two female *M. fasciiventris* and two female *M. jucundus* being used. Each insect was retained in the box for four consecutive days, observations being made for an hour on each day, this being the only time the box was illuminated. The insects fed from a small wad of cotton wool soaked in honey-water placed in a corner of the box. The results are shown in Table II, and they indicate that *M. fasciiventris* is

TABLE II.—*The attention paid by* M. fasciiventris *and* M. jucundus *to different sizes of plasticine balls*

Diameter of plasticine balls (mm.)	Number of times approached by *M. jucundus* Expt. 1	*M. jucundus* Expt. 2	*M. fasciiventris* Expt. 3	*M. fasciiventris* Expt. 4
1	4	2	16	9
2	3	5	29	10
3	5	4	16	10
4	3	6	14	4
5	9	8	11	7
6	12	11	7	5
7	4	8	5	3
8	10	8	4	5
9	3	6	3	5
10	5	9	5	.

A chi-square test on the above figures gave $P < 0{\cdot}001$ that *M fasciiventris* preferred balls 5 mm. and less in diameter, whereas *M. jucundus* preferred balls 6–10 mm. in diameter.

more attracted by small objects while *M. jucundus* is more attracted by larger objects.

M. fasciiventris is generally a smaller insect than *M. jucundus*, the average length of 20 females being 2·59 mm., as opposed to 3·03 mm. for *M. jucundus*. The ovipositor lengths of specimens of these sizes were found to be 1·26 mm. for *M. fasciiventris* and 1·40 mm. for *M. jucundus*. This difference in ovipositor length is insufficient to account on a mechanical basis for the different distributions of the species among galls of different sizes. Both species were found in the inquiline cells of *Synergus pallicornis* Htg., which lie in the peripheral cell wall of *Cynips* galls, often at a depth of less than a millimetre.

The difference in the average lengths of the ovipositors of these two species may, however, account for the apparent difference in distribution of the species inside *Cynips* galls, as ascertained by rearing larvae to adult insects. *M. jucundus* predominates in the main cells of these galls, where it was found eight times as opposed to twice for *M. fasciiventris*. *M. fasciiventris*, however, was found in inquiline cells of *Synergus pallicornis* on nine occasions as against six for *M. jucundus*.

(iii) *Gall position.*—The apparent absence of *M. fasciiventris* from *A. kollari* galls (Table III) cannot be completely explained by the usual large size of this gall (mean diameter 14·4 mm.), because some galls attacked at an early stage of growth by *Synergus reinhardi* Mayr do not exceed 5 mm. in diameter, and *C. divisa* galls of this size are sometimes attacked by *M. fasciiventris*.

In the field *M. jucundus* was observed to search the oak branches by examining leaves and twigs more or less alternately, and only use its wings to carry it to a fresh branch after the first one had been well investigated. *M. fasciiventris*, on the contrary, was frequently seen to fly from leaf to leaf, and was seldom observed walking

on twigs. A laboratory experiment gave some support to this field observation on the neglect of twig searching by *M. fasciiventris*. A female *M. fasciiventris* and a female *M. jucundus* were placed in turn on an oak sprig composed of three twigs and bearing 20 leaves. The female *M. fasciiventris* spent 105 seconds searching leaves but only 5 seconds searching twigs; the female *M. jucundus* spent 250 seconds searching leaves and 146 seconds searching twigs.

The host–gall list of *M. fasciiventris* (Table I), which includes galls of ten species, is made up entirely of leaf galls. Bud galls are apparently not attacked[2], and the

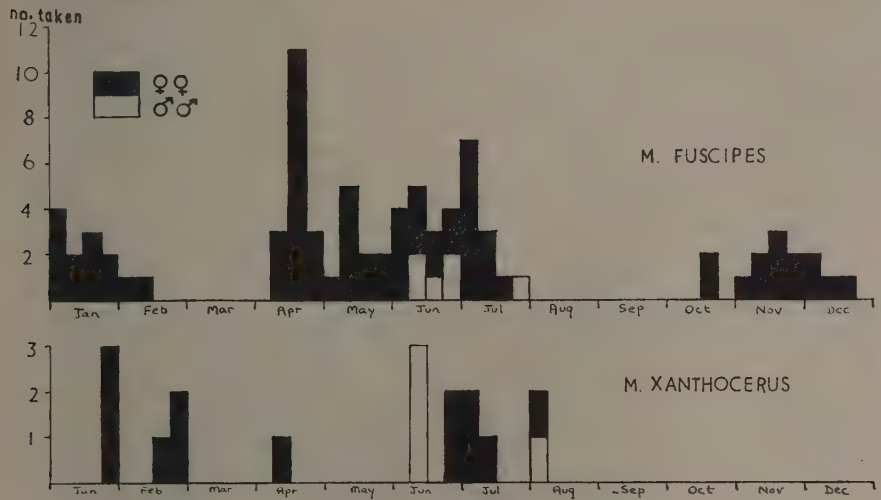


FIG. 9.—Field captures of *Mesopolobus fuscipes* (Walk.) and *M. xanthocerus* (Thoms).

species spends very little time on twigs. In contrast, the host–gall list of *M. jucundus* includes six leaf galls and five bud galls.

(2) Mesopolobus fuscipes (*Walker*)

The life-cycle and field captures of *M. fuscipes* are shown in figures 8 and 9 respectively. It shares with *M. xanthocerus*, and possibly *M. dubius*, the unusual habit among oak-gall parasites of overwintering as an adult insect outside the gall. Many female *M. fuscipes*, caught in Oak Survey oak-trunk nets in winter, have been examined. Only the females hibernate and they then have immature ovaries and well-developed fat bodies. The place of hibernation is among the clusters of small twigs and debris found at the bases of the boles of some mature oak trees, from which situation three females were beaten on February 5th, 1960. The species was not beaten in the winter from conifers, which provide hibernation sites for many Chalcidoid species (e.g. *M. xanthocerus*). The winter captures of *M. fuscipes* in oak-trunk nets indicate that it is merely in a state of reduced activity rather than in true hibernation.

The females become more active early in spring. Eggs were first found in the ovaries of females taken in early April in oak-trunk nets and on female *Salix* flowers. In April and May many *M. fuscipes* were found drilling and investigating oak buds before the leaves were on the trees. Drilled buds were dissected under a binocular microscope. No galls could be found in some, but others contained young galls of

[2] Since preparing this paper, I have had a single male *M. fasciiventris*, together with 15 male and 14 female *M. jucundus*, emerge from a collection of 13 *A. kollari* galls from Wytham Wood, 1960. Thus the avoidance of bud galls by *M. fasciiventris* is not absolute.

N. albipes, *N. aprilinus* (Gir.) and *A. ostreus* f. *furunculus* (Bey.). On May 21st, 1958 a female *M. fuscipes* was observed drilling into a gall of *N. albipes* situated on the margin of a small leaf. This is the only occasion on which *M. fuscipes* was observed attacking a gall not in a bud. Collections of galls of *N. aprilinus*, *N. albipes*, *N. numismalis* f. *vesicator*, *A. ostreus* f. *furunculus*, *A. kollari* f. *circulans* Mayr, (?) *A. callidoma* f. *cirratus* Adler, *C. longiventris* f. *substituta* Kinsey and *C. quercus-folii* f. *taschenbergi* (Schl.) yielded *M. fuscipes* from the end of May to the beginning of July. The record from the gall of *A. callidoma* f. *cirratus* is based on the contents of a dried up *Mesopolobus* pupa which appeared to be a female *M. fuscipes*.

The host galls of *M. fuscipes* are all early or very early in time of appearance. They are nearly always attacked while still enclosed by bud scales. Those that are bud galls proper, always remaining small and often at least partially enclosed by bud scales (*N. aprilinus*, *N. albipes* (some), *A. kollari* f. *circulans*, *A. ostreus* f. *furunculus*, *C. longiventris* f. *substituta*, *C. quercus-folii* f. *taschenbergi*), are most heavily attacked by *M. fuscipes*. Those that begin their development in the bud, but grow to their fullest extent on expanded leaves (*A. curvator*, *N. numismalis* f. *vesicator*) or catkins (*A. callidoma* f. *cirratus*), are only occasionally attacked. The galls of *A. kollari* f. *circulans* grow only on *Quercus cerris*. The buds containing the host galls of *M. fuscipes* may be on the twigs (e.g. *N. aprilinus*) or growing on the bole of the tree (e.g. *C. longiventris* f. *substituta*). The insects which emerge from these galls are of both sexes and are on oak in June and July. There may be some temporal overlap between these adults and the females that have overwintered. *M. fuscipes* was not bred from any gall later in the year than July, nor were females found ovipositing in the year of their emergence. Females taken in the field from June onwards had immature ovaries and large fat bodies. The insects which emerge from spring galls must be the same as those which overwinter; in other words *M. fuscipes* has only a single generation during a year. However, the single male captured in the field on July 24th, 1958 (fig. 9) may represent a partial second generation. In August and September *M. fuscipes* leaves the oaks. During this period females with immature ovaries were beaten from spruce (*Picea*). Mating presumably occurs soon after emergence, and the males then die.

Overwintering as an adult insect outside the gall enables *M. fuscipes* to be in flight from the earliest days of spring, and to attack the very early galls of, for example, *N. aprilinus* and *C. longiventris* f. *substituta*, which no other *Mesopolobus*, except *M. xanthocerus*, would be capable of doing. *M. fuscipes* goes a stage further than *Olynx* and *Ormocerus* species, which overwinter as fully formed adults still within the pupal skin. The preference of *M. fuscipes* for bud galls, and usual avoidance of leaf galls, prevents it from coming into complete competition with *M. tibialis*, which is the other abundant spring *Mesopolobus* species in Wytham Wood. Only in the galls of *N. albipes*, which may develop either on the edge of a leaf or on stunted leaves remaining partially enclosed by bud scales, are both species present in large numbers.

Breeding records of *M. fuscipes* are included in Table III.

(3) Mesopolobus tibialis (*Westwood*)

The life-cycle and field captures of *M. tibialis* are shown in figures 8 and 10 respectively. Close to *M. fuscipes* in adult morphology, *M. tibialis* differs biologically from that species in having two generations, and sometimes (*e.g.* 1959) partially three, during a year. It does not overwinter as an adult insect, but usually as a fully-grown larva. Its overwintering host galls are the spangle galls of *Neuroterus* from which insects of the first generation emerge in spring and are in flight in May and early June. On June 6th, 1958 a female *M. tibialis* of this spring generation was found drilling into a gall of *N. numismalis* f. *vesicator* and second generation

TABLE III.—*Numbers of* Mesopolobus *species bred from Cynipid galls on oak*

Gall position and season of formation	Host galls	*fuscipes*	*tibialis*	*dubius*	*amaenus*	*xanthocerus*	*albitarsus*	*fasciiventris*	*jucundus*
Spring, leaf of catkin	*N. q.-baccarum*	.	8	.	.	.		.	2
Spring, leaf	*N. tricolor*	.	4	.	.	.	.	.	.
	N.n. f. *vesicator*	1	53	.	.	.	.	19	.
	A. curvator	1	5	.	1	.	2	9	18
Spring, leaf or bud	*N. albipes*	45	102	.	.	.	.	5	.
Spring, bud	*A. o.* f. *furunculus*	49	2	.	.	1	.	.	.
	A. k. f. *circulans*	40	.	.	.	6	.	.	.
	N. aprilinus	8	.	.	.	.	.	.	.
	C. l. f. *substituta*	1	.	.	.	.	.	.	.
	C. q.-f. f. *taschenbergi*	1	.	.	.	.	.	.	.
	A. albopunctatus	.	5	.	.	.	.	.	.
	B. pallida	.	6	2	37	13	.	.	53
Spring, catkin	*A. c.* f. *cirratus*	1 ?	.	.	.	.	.	.	.
	A. quadrilineatus	.	.	.	.	3	.	.	.
	A. f. f. *pilosus*	.	.	.	.	2	.	.	.
Summer, leaf	*A. ostreus*	.	.	.	.	.	.	60	4
	C. divisa	.	.	1	.	.	.	153	54
	C. q.-folii	.	.	.	.	.	.	7	5
	C. longiventris	.	.	.	.	.	.	21	7
Summer, bud	*A. kollari*	.	.	.	2	.	.	.	76
	A. solitarius	.	.	.	4	.	.	.	1
	A. callidoma	.	.	.	.	.	.	.	1
Autumn, leaf	*N. a.* f. *laeviusculus*	.	2	.	.	.	.	1	.
	N. numismalis	.	9	.	.	.	.	3	.
	N. q.-b. f. *lenticularis*	.	5	1	.	.	.	1	.
Autumn, bud	*A. i.* f. *globuli*	.	.	.	.	.	.	.	1
	A. c. f. *collaris*	.	.	.	2	.	.	.	.

insects have been bred later in the year from galls of this species and of *N. quercus-baccarum*, *N. tricolor* (Htg.), *A. ostreus* f. *furunculus*, *A. albopunctatus* (Schl.), *A. curvator* and *B. pallida*.

Insects of the second generation are in the field in the latter half of June and in July. There may be a slight overlap of flight periods with the first generation. Constant watching in the field during these months failed to discover any ovipositing females of the second generation of *M. tibialis*, and on dissection the females caught in late June and in July were found to have immature ovaries. In the second half of July, and in August, *M. tibialis* were seldom found on oak, and they probably fed at other vegetation during this period. On August 16th, 1958 a female *M. tibialis* was found feeding at a flower of Sea Holly (*Eryngium maritimum* L.) on the sand dunes of Jersey, Channel Islands, over a mile from the nearest oak tree. On August 7th, 1959 a female *M. tibialis* was beaten from oak in Wytham Wood. It had a larval Trombid mite (?*Atomus parasiticus* (De Geer)) attached to its thorax and Dr. G. Owen Evans, who kindly determined the mite, informs me that it was probably picked up from flowers by the Chalcid.

Second generation *M. tibialis* return to the oak trees in September and persist into November or even (1959) December. With two exceptions, discussed below, all the *M. tibialis* caught at this time were females, and their ovaries contained ripe eggs in contrast to the condition of *M. fuscipes* at this time. Mating of the second generation must occur in June and July, probably before the insects leave the oaks. Second generation males do not return to the oaks. The mild, dry autumn of 1959

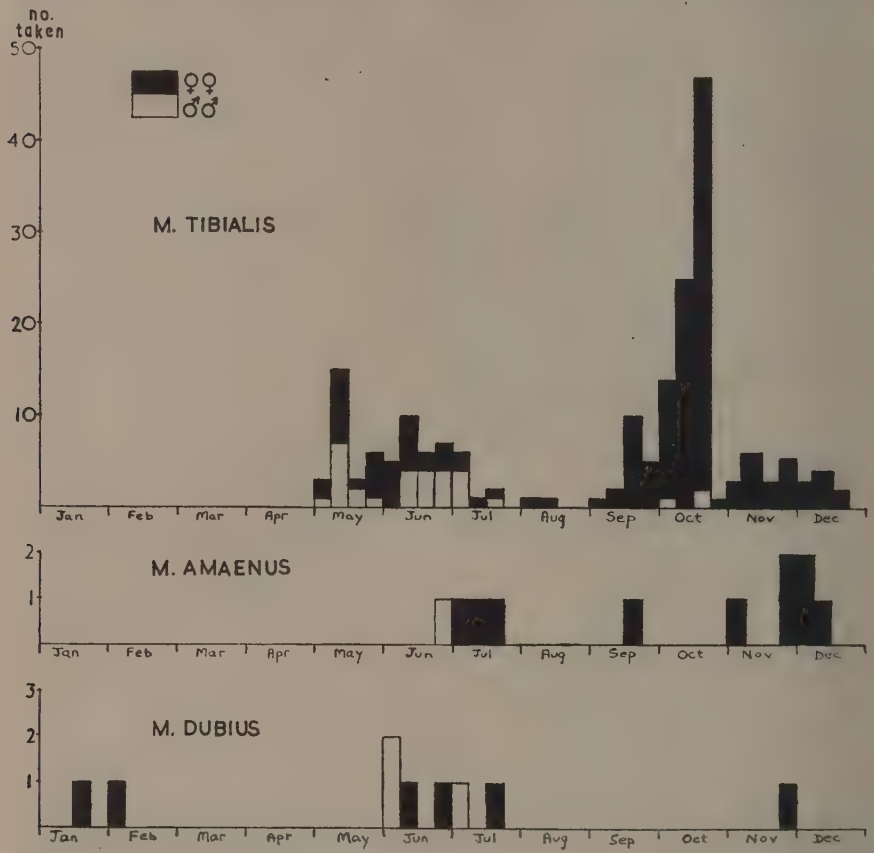


FIG. 10.—Field captures of *Mesopolobus tibialis* (Westw.), *M. amaenus* (Walk.) and *M. dubius* (Walk.).

induced the emergence of a partial third generation, actually equivalent to the first generation of 1960. On October 22nd, 1959 there appeared in a ground trap of the Oak Survey in Wytham Wood, one male and three female *M. tibialis*. The trap had been laid in July but had been moved in autumn to a new position. In its second position it must have encompassed some newly fallen spangle galls containing *M. tibialis*. In a normal year these would probably not have emerged until the following spring. Two male *M. tibialis* were taken on oak in October, 1959, and these also must have been "forced" representatives of the spring generation. Female *M. tibialis* were found drilling into spangle galls in September and October. Three were found attacking galls of *N. numismalis* and seven galls of *N. quercus-baccarum* f. *lenticularis*. The offspring of these females emerged the following spring as the first generation.

To summarise the life-cycle of *M. tibialis*, the first generation emerges in spring from spangle galls of *Neuroterus* and attacks the spring galls of a large number of oak Cynipidae. The second generation emerges in the summer from these galls and leaves the oaks after mating. The females probably frequent flowers and they return to the oaks in autumn to attack spangle galls. They overwinter as fully grown larvae.

The spring galls attacked by *M. tibialis* are mostly leaf galls (*A. curvator*, *N. numismalis* f. *vesicator*, *N. quercus-baccarum*, *N. albipes*, *N. tricolor*). Bud galls (*A. kollari* f. *circulans*, *A. albopunctatus*, *B. pallida*, *A. ostreus* f. *furunculus*) are only occasionally attacked. Catkin galls do not appear to be attacked by *M. tibialis*. The species has not been reared from catkin galls of *N. quercus-baccarum*.

Breeding records of *M. tibialis* are contained in Table III.

More than one *M. tibialis* may successfully develop from single galls of *A. albopunctatus* and *N. quercus-baccarum* when these galls contain *Synergus* which have divided the single main cell into a number of subsidiary cells.

M. tibialis larvae have been found feeding on : *N. quercus-baccarum* f. *lenticularis* larvae, *N. albipes* f. *laeviusculus* larva, *N. numismalis* larva, *N. albipes* larvae, *N. tricolor* larvae and pupae, *N. numismalis* f. *vesicator* larvae and pupae, *Synergus gallaepomiformis* (Fonsc.) larvae (*A. albopunctatus*, *N. quercus-baccarum* galls), *S. albipes* Htg. larvae (*N. numismalis* f. *vesicator*, *N. tricolor* galls), *Caenacis divisa* (Walk.) larva (*A. albopunctatus* gall), *Pediobius* (=*Pleurotropis*) *lysis* (Walk.) larva (*N. numismalis* gall) and larvae of its own species (*N. quercus-baccarum* gall).

Von Rosen (1958) mentions that *M. tibialis* has been bred from the larvae of *Tortrix viridana* (L.), and refers to Silvestri (1923) and Seabra *et al.* (1924). Silvestri records breeding 16 female and 5 male *M. tibialis* from a single chrysalis of *T. viridana* on June 29th, 1917. There can be little doubt that these records are incorrect, involving either misidentification of the Chalcids or faulty rearing technique. If the *Tortrix* were collected as pupae in rolled-up leaves, Cynipid galls could very easily be included with them. Silvestri figures his *Eutelus* (=*Mesopolobus*) *tibialis* and depicts the female antenna with five funicle segments, two large annelli approximately equal in size but considerably smaller than the first funicle segment, and a single small annellus. In *M. tibialis* there are two small annelli and the third annellus is almost as large as the first funicle segment, so that the funicle appears to be six-segmented. Silvestri's figure disagrees with *M. tibialis* in other small features also.

(4) Mesopolobus xanthocerus (*Thomson*)

M. xanthocerus appears to have, like *M. fuscipes*, only one generation (fig. 9) during a year, which overwinters as adult insects outside the galls. Three females with immature ovaries were beaten from *Picea* in Wytham Wood on January 29th, 1960 and three more in February. *M. xanthocerus* was bred from the early spring galls of *A. quadrilineatus* Htg., *A. ostreus* f. *furunculus* and *A. kollari* f. *circulans*, which confirms the existence of an early flight period, as in *M. fuscipes*. *M. xanthocerus* was also bred from galls of *B. pallida*, and specimens bred from galls of *A. fecundator* f. *pilosus* Adler were examined in the British Museum (Nat. Hist.). *M. xanthocerus*, like *M. fuscipes*, apparently leaves the oaks on emergence in summer and it does not return until the following spring. Two females were taken on *Picea* on July 13th, 1959 and another on August 4th, 1959.

The available data show *M. xanthocerus* to have a similar life-cycle to *M. fuscipes*, but it attacks catkin galls (*A. quadrilineatus*, *A. fecundator* f. *pilosus*) as well as bud galls. The oak-apple gall of *B. pallida* is also attacked by *M. xanthocerus* and not *M. fuscipes*. This gall is initially a bud gall but it very soon grows completely out of the bud scales.

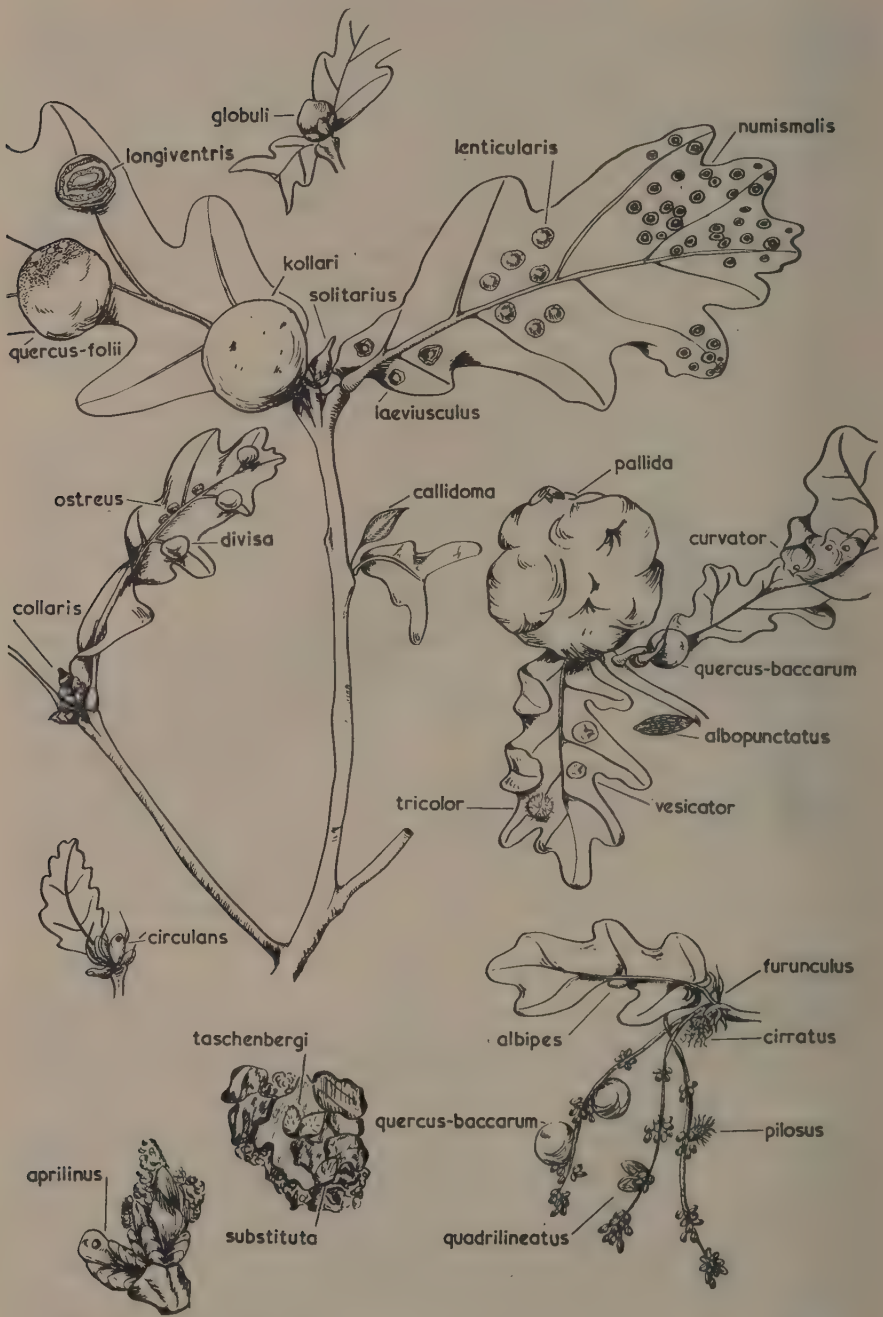


FIG. 11.—Cynipid oak galls, the contents of which are attacked by species of *Mesopolobus*.

Breeding records of *M. xanthocerus* are included in Table III.

M. xanthocerus was found to have fed on larvae of *Olynx euedoreschus* (Walker) and the gall maker in galls of *A. quadrilineatus*.

(5) Mesopolobus dubius (*Walker*)

A male *M. dubius* was obtained in April, 1959 from a gall of *C. divisa* gathered at Cothill, Berkshire, in November of the previous year. Another male emerged in a heated room in February, 1959 from a gall of *N. quercus-baccarum* f. *lenticularis* gathered at Gosforth, Northumberland in the previous December.

In the British Museum (Nat. Hist.) a male and a female *M. dubius* are labelled as emerging from galls of *B. pallida* collected at Oxshott Heath, Surrey by D. M. S. Perkins in June, 1952. The male emerged later in June and the female in July, 1952.

These few records of the breeding of this species suggest that it has a similar life-cycle to *M. tibialis*, and overwinters as a larva in galls. However, the dates of field captures (fig. 10) do not altogether fit in with this opinion. There is a first-generation flight period in early June which corresponds with the emergence from *N. quercus-baccarum* f. *lenticularis* and *C. divisa* galls. The second generation is in flight in late June and in July, corresponding to the emergence from galls of *B. pallida*. The species then apparently leaves the oaks until late in the year, but it does not disappear by the end of the year as do female *M. tibialis*. Females with ripe eggs in their ovaries were caught in oak–trunk nets throughout the winter up till February in 1960. Thus some females may pass the winter as adult insects, although the condition of the ovaries suggests that the females taken in the winter had already oviposited in autumn ; all Chalcids certainly known to overwinter as adults in order to oviposit in spring do so with immature ovaries. The males of *M. dubius* undoubtedly overwinter in galls, probably as fully-grown larvae. More records of *M. dubius* are required to clarify the life-cycle.

(6) Mesopolobus amaenus (*Walker*)

Figure 10 shows the dates of field captures of this species. *M. amaenus* overwinters in galls, probably as a fully-grown larva. It was bred in spring from the gall of *A. curvator* f. *collaris* (Htg.) and specimens bred in March from *A. kollari* galls, gathered by P. Atkins at Morden, Surrey, have been examined in the British Museum (Nat. Hist.). Overwintering insects attack, on their emergence, galls of *A. curvator*, *A. solitarius* and *B. pallida*. The flight periods of *M. amaenus* on oak correspond with those of *M. tibialis*, the autumnal generation lasting into December. One of the December specimens was beaten from dead oak leaves still attached to the tree ; others were caught in oak-trunk nets. Galls of *A. curvator* f. *collaris* which have been attacked by *Synergus* remain fastened to the tree for much of the winter and the late females may have been searching for these galls.

The usual summer host gall is that of *B. pallida*. The insects which emerge from this gall in July may attack another host gall to produce the autumnal generation, but it seems more likely that the females leave the oaks and return in autumn, as with *M. tibialis*.

Except for the single record from a gall of *A. curvator*, *M. amaenus* has only been bred from bud galls. Breeding records are given in Table III.

An egg of *M. amaenus* (the adult was reared) was found on a paralysed larva of *A. curvator* f. *collaris*. A specimen from Morden, Surrey, in the British Museum (Nat. Hist.), is labelled as emerging from a cell of *Synergus umbraculus* (Oliv.) in a gall of *A. kollari*.

Eutelus lichtensteini Mayr, synonymised with *M. amaenus* by von Rosen (1958), is recorded (Frediani, 1955, 1959) as a parasite of the Cecidomyid fly *Dryomia lichtensteini* Loew, which galls leaves of *Quercus ilex* L. in southern Europe. Dr. Frediani has been kind enough to send me some of his material of *M. amaenus* bred from *Dryomyia* galls. These specimens differ from those bred from Cynipid oak galls in their much smaller size, narrower pronotal collar and absence of a dark band on the male funicle. They may well represent a distinct species.

(7) Mesopolobus albitarsus (*Walker*)

This species is very rare in Wytham Wood and probably elsewhere in the country. The author knows of it only from two females in Mr. G. R. Gradwell's collection, both labelled "Em. 2.vii.1952. ex *A. curvator*. Wytham, Berkshire. G. R. Gradwell"; and two females taken on oak by Dr. M. W. R. de V. Graham on July 31st, 1952 and July 19th, 1953.

V. Discussion

The gall-inhabiting *Mesopolobus* are interesting ecologically in that several congeneric species, all parasites in oak galls, occur in the same area. According to Gause's Theorem, these species must differ ecologically in order to persist together, and such an ecological differentiation was, in fact, found. All the species are polyphagous and it is not the contents of the galls, but their position, form and season of growth that are important in determining which galls are attacked by which *Mesopolobus* species. Each species of *Mesopolobus* has a range of host galls which more or less overlaps with the host gall range of one or more of the other species, but where sufficient information is available it is seen that each species has its own distinct "preferendum". These preferenda may be summarised as follows:

M. fasciiventris—small leaf galls, but seldom spangle galls.
M. jucundus—larger leaf galls and bud galls.
M. tibialis—leaf galls (the second generation attacks only spangle galls), and occasionally bud galls.
M. fuscipes—early bud galls (excluding oak-apple galls).
M. xanthocerus—early bud galls (including oak-apple galls), and catkin galls.
M. amaenus—bud galls.

Further differentiation is found in the life-cycles, of which there are three types:

Species having one flight period annually and overwintering as adults. (*M. fuscipes* and *M. xanthocerus*.)

Species having two flight periods annually and overwintering as fully-grown larvae. (*M. tibialis* and probably *M. amaenus* and *M. dubius*.)

Species having three flight periods annually and overwintering as fully-grown larvae. (*M. fasciiventris* and *M. jucundus*.)

Thompson and Parker (1927), in a consideration of the host relations of polyphagous parasites, conclude that there is "no reason to suppose that the accumulation of data on the host relations of entomophagous parasites will ever lead to the discovery of laws of parasite distribution permitting us to correlate the properties of parasites with those of their hosts so that we can predict in advance the host list of a given parasite or the parasitic fauna of a given host". The establishment, in the present work, of characters which determine the liability of oak galls to be attacked by a given species of *Mesopolobus*, has shown this opinion to be unduly pessimistic.

VI. Summary

Eight British species of *Mesopolobus* pass their immature stages, which are described where known, in oak Cynipid galls, in which they are polyphagous ectoparasites of other gall inhabitants.

M. fasciiventris and *M. jucundus* are attracted to their host galls by visual stimulation in the first instance, although some inconspicuous galls are apparently discovered by chance. The olfactory sense plays little or no part in attracting the parasites to host galls, but galls are probably distinguished from other objects by antennal chemoreceptors.

Interspecific destruction in the gall-inhabiting *Mesopolobus* is minimised by the adoption of a different host gall range by each of the species, though there is some

overlapping of the host–gall ranges. A gall's form, time of growth and position on the tree determine its liability to be attacked by a given species of *Mesopolobus*.

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